

**AZTECASTER (ASTERACEAE: ASTEREA), A NEW DITYPIC GENUS OF
DIOECIOUS SHRUBS FROM MEXICO WITH REDEFINITIONS OF THE
SUBTRIBES HINTERHUBERINAE AND BACCHARIDINAE**

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ABSTRACT

Aztecaster, *gen. nov.*, comprises two species endemic to México: *A. pyramidatus* (B. Robins. & Greenm.) Nesom, of Oaxaca, and *A. matudae* (Rzed.) Nesom, of San Luis Potosí, Zacatecas, Coahuila, and Nuevo León. Both species are glutinous, dioecious shrubs with white-pannose stems, ericoid leaves, heads in an open-spicate capitulescence, and flat achenes. They are the only dioecious species of Astereae not included in the subtribe Baccharidinae, where this sexual condition apparently has been independently derived. Most recently, the two species of *Aztecaster* have been treated as *Baccharis*, but based on features of vegetative, capitular, floral, and fruit morphology, they are more closely related to the North American genus *Ericameria* and a group of genera centered primarily in South America but also reaching Australasia and Africa. This is the subtribe Hinterhuberinae, originally described by Cuatrecasas but amended here to include about 20 genera of the Southern Hemisphere (e.g., *Chiliotrichum*, *Diplostephium*, *Hinterhubera*, *Pteronia*, *Rochonia*, and *Olearia*), in addition to the two North American ones (*Aztecaster* and *Ericameria*). The subtribe Baccharidinae is redefined to include five primarily Afro-Madagascan genera (*Microglossa*, *Psiadia*, *Psiadiella*, *Sarcanthemum*, *Vernoniopsis*) in addition to the three New World genera (*Baccharis*, *Archibaccharis*, *Heterothalamus*) of previous classifications.

KEY WORDS: *Aztecaster*, *Ericameria*, *Baccharis*, Astereae, Hinterhuberinae, Baccharidinae, Asteraceae, dioecy

Recent studies of the genera *Ericameria* Nutt. and *Chrysothamnus* Nutt. (Nesom 1990a; Nesom & Baird 1993; Baird in prep.) focus attention on anomalous species both previously and now included in those groups. One such

species excluded from *Chrysothamnus* has most recently been treated within *Baccharis* L. as *B. pyramidata* (B. Robins. & Greenm.) Rzed. (Rzedowski 1972), but even in the latter genus it has remained a peculiarity. In a taxonomic overview of the North and Central American species of *Baccharis* (Nesom 1990b), *B. pyramidata* was tentatively included in *Baccharis* sect. *Glandulocarpae* Nesom "largely on the basis of its similarity in habit and capitulescence to *B. pteronioides* [DC.], but its stiffly strigose achenes and peculiar ericoid leaf morphology are anomalous among the Mexican species. The species of the South American sect. *Discolores* DC. are similar in leaf morphology but have a different capitulescence as well as details of the phyllaries and achenes" (p. 43).

In addition to transferring *Bigelovia pyramidata* to *Baccharis*, Rzedowski (1972) described a related but geographically separate and morphologically distinct species as *Baccharis matudae* Rzed. In some earlier studies I annotated specimens of the latter as *Baccharis pyramidata* but now recognize that there are indeed two species. In the following discussion, these two are referred to as the "pyramidata pair."

Plants of *Baccharis pyramidatus* were first described as a species of *Bigelovia* DC. by Robinson & Greenman (1896), apparently following Asa Gray's broad concept of that genus (1884), which included shrubby species now apportioned primarily among *Ericameria*, *Chrysothamnus*, and *Isocoma* E. Greene. Its original authors described *Bigelovia pyramidata* as "anomalous in its spicate-paniculate inflorescence but with the other characters of *Bigelovia*" (p. 43), but apart from this observation and the formal description, they provided no other comments regarding its relationship. In their resegregation and consolidation of *Chrysothamnus*, Hall & Clements (1923) removed from Gray's *Bigelovia* a group of species, including *Bigelovia pyramidata*, that they regarded as constituting *Chrysothamnus*. Their primary criteria for recognizing the latter genus were discoid and cylindrical heads and alignment of phyllaries (involucral bracts) in vertical ranks (see further comments in Nesom & Baird 1993). Hall & Clements described the phyllaries of *C. pyramidatus* (B. Robins. & Greenm.) Hall & Clements, however, as having "ranks obscure" and noted (p. 197) that "The exact position of *C. pyramidatus* in the genus is not certain, but it is placed in the [sect.] *Nauseosi* because of the pannose tomentum of the twigs. The decidedly spicate or subracemose inflorescence is suggestive of a remote relationship with *C. parryi*." They provided no other comments regarding the taxonomy of *C. pyramidatus*, but they placed it basally in sect. *Nauseosi* (their Fig. 25), coordinate in position with the other two species, noting (p. 164) that it "separated from the original stock [of sect. *Nauseosi*] in early times." Blake's subsequent transfer of the species to *Haplopappus* (1926) was not accompanied by any comment, but he returned it to a large, diverse genus, one that included most of Gray's *Bigelovia* and more. In Blake's key, however, the species was identified in the vicinity of species of *Ericameria*.

It was not until 1972 that Rzedowski discovered *Bigelovia* (or *Chrysothamnus*) *pyramidata* to be dioecious and that the previous descriptions and assessments of its taxonomic position had been based on plants bearing heads with only staminate flowers. His ensuing decision to place it in *Baccharis* was reasonable, as dioecious species of *Astereae* have previously been reported only in this and two other closely related genera of American *Baccharidinae* (see below). The species has been excluded from *Chrysothamnus* in recent studies (e.g., Anderson 1986) in favor of a position in *Baccharis*. The only other comment that I am aware of regarding this species is from an informal study and specimen annotation by B.L. Turner in 1976 (before he was aware of Rzedowski's publication); Turner noted that it is similar to species of *Haplopappus* that are now treated within the genus *Ericameria* (Nesom 1990a).

As observed by Rzedowski (1972) and Nesom (1990b), the ericoid leaves of *Baccharis pyramidata* are similar to those in some species of South American *Baccharis* sect. *Discolores*. While *Baccharis* is highly diverse in vegetative morphology and the arrangement of heads, resulting in the recognition of about 20-25 formally described sections, the genus is considerably more uniform in features of its phyllaries, flowers, and achenes. In all species of *Baccharis* (with reference to *B. pyramidata*), the phyllaries are more foliaceous, never completely indurated, the apex of the pistillate corollas is represented by a single, small ligule or the tube is apically truncate and merely fimbriate, the sinuses of the staminate corolla lobes are cut nearly to the base of the throat, the staminate style branches are relatively short with abruptly obtuse apices, and the achenes are mostly 0-1.5 mm long, rarely longer, terete or slightly compressed, never flattened, usually glabrous to moderately strigose, uncommonly with glands, and produce 5-11 ribs or nerves. Two other dioecious or polygamo-dioecious genera of American *Baccharidinae*, *Archibaccharis* Heering and *Heterothalamus* Less., are essentially similar to *Baccharis* in these features, except for the staminate corollas of *Heterothalamus*, which have short lobes.

Baccharis pyramidata and *B. matudae* are anomalous in all of the features noted above as characteristic of *Baccharidinae*. The heads of these species have strongly indurate phyllaries, actinomorphic pistillate corollas with five apical lobes, staminate corolla lobes with sinuses cut about halfway to the base of the throat, staminate styles with long, strongly tapering branches and appendages, and achenes that are mostly 2.5-3.0 mm long, distinctly flat with two lateral nerves, and moderately to densely strigose. If these two species are to be included in *Baccharis*, they would have to be placed in a subgeneric taxon coordinate in rank with all of the rest of the genus. Alternatively, in their shrubby habit, production of resin, pannose vestiture, narrow ericoid leaves, discoid heads, the morphology of the style branches of the staminate flowers (stigmatic lines absent, concomitant with ovary sterility), and achene morphology, *B. pyramidata* and *B. matudae* have a strong overall similarity to plants of the genus *Ericameria* Nutt. Such a similarity clearly led to the

earlier classification of *B. pyramidata* near species of *Ericameria*, prior to its alignment with *Baccharis*.

The placement of *Bigelovia pyramidata* in *Chrysothamnus* by Hall & Clements (1923) presumably (though unstated by them) was on the basis of their overall similarity and particularly because of their common production of vertically aligned phyllaries. While *Ericameria* and *Chrysothamnus* apparently are phylogenetically distant from each other (see Nesom & Baird 1993), differences between the two are obscured by convergence in many of the morphological features that serve to separate them. The placement of the pyramidata pair in one or the other of these genera would be correspondingly problematic, but the open-spicate capitulescence, long, tapering style branches, and relatively short, flat, few-nerved achenes are features characteristic of *Ericameria* rather than *Chrysothamnus*. Further, this species would be anomalous within *Chrysothamnus* (Baird in prep.). The species of sect. *Nauseosi*, where Hall & Clements originally placed *B. pyramidata*, are now transferred to *Ericameria* (Nesom & Baird 1993).

Baccharis pyramidata and *B. matudae* would also be isolated within *Ericameria*. The geographical range of this pair is completely separate from that of the 31 species of *Ericameria*, which have radiated entirely in the western and southwestern United States and adjacent México. Ericoid leaves are characteristic of sect. *Ericameria* and the pyramidata pair, but in contrast to those of the latter, leaves within sect. *Ericameria* are punctate-glandular. The pyramidata pair are similar to *Ericameria* sect. *Asiris* (H.M. Hall) Nesom in their keeled phyllaries without an orange midvein and their flattened and few-nerved achenes; they are similar to *Ericameria* sect. *Macronema* (H.M. Hall) Nesom in their pannose stem vestiture, heads in a spicate capitulescence immediately subtended by leaves. Their phyllaries lack a distinct apical apiculum or foliar appendage, which is characteristic of the latter two sections, and no approach to the dioecism of the pyramidata pair is found in *Ericameria*.

An examination of the ca. 185 genera of the tribe Astereae shows that the evolutionary relationships of the pyramidata pair can be placed within a broader context. These two species and those of *Ericameria* are part of a significantly larger generic group, here referred to as the subtribe Hinterhuberinae (Table 1). Here also, the geographical isolation, morphological distinctiveness, and the dioecy of the pyramidata pair provide the basis for treating these two species as the new genus *Aztecaster* (see below).

REDEFINITION OF THE SUBTRIBE HINTERHUBERINAE

Cuatrecasas (1969) erected the monotypic Hinterhuberinae to include the species of *Hinterhubera*, which are shrubby plants with sterile disc ovaries and regularly to irregularly lobed pistillate (peripheral) corollas (Cuatrecasas &

Aristeguieta 1956). He later (1986) expanded the group to include the herbaceous genera *Westionella* Cuatr., *Flosmutisia* Cuatr., and *Blakiella* Cuatr., which have similar peripheral corollas and sterile disc ovaries, but these belong in a clade apart from *Hinterhubera* (Nesom in prep.), as do two other herbaceous genera added to the "*Hinterhubera* group" by Zhang & Bremer (1993). The *Hinterhuberinae* as defined by Cuatrecasas was rejected by Zhang & Bremer, but upon the recognition of the wider generic relationships of *Hinterhubera*, it becomes the correct name for the group as a subtribe, here considered its appropriate rank. The generic composition of the subtribe, based on my morphological studies of the *Astereae*, is outlined in the present paper (Table 1), but a more detailed phylogenetic and taxonomic review is in preparation.

The *Hinterhuberinae* as a group is recognized by the following set of features. All except *Oritrophium* are shrubs. Most produce a dense, close, and persistent ("pannose") tomentum on the stems and leaves, and they produce leaves that are evergreen, coriaceous, commonly ericoid in morphology (linear to much broader but almost always with revolute margins and a raised abaxial midrib), and punctate in some of the American genera. Some species of *Ericameria* have thinner leaves. All of the South American genera except *Lepidophyllum*, *Parastrephia*, and *Hinterhubera* have at least some species that produce receptacular bracts (pales). The disc corolla lobes are commonly long but variable in length and the collecting appendages of the disc style branches also are highly variable in length. The ray corollas are primarily yellow but white to pink or blue in some (*Chiliotrichum*, *Diplostephium*, *Oritrophium*, the *Olearia* group, and the "asters" of Madagascar; there is a tendency for loss of ray flowers. The achenes are relatively large, commonly glandular, multi-nerved, and have a strong tendency to be nearly terete in outline, although distinctly flattened achenes also occur. The group has a remarkable geographic distribution: Madagascar, South Africa, South America, North America, and Australasia.

The largest subgroup within the *Hinterhuberinae*, the South American *Chiliotrichum* group, comprises a number of small genera endemic primarily to the southern Andean region, although it extends northward. It has been recognized in various taxonomic stages (Blake 1930; Cabrera 1937, 1944, 1945, 1953, 1954; Zhang & Bremer 1993). I suggested earlier (Nesom 1991) that part of this group might be included within the *Solidagininae* but now view the latter as much more distantly related to the *Hinterhuberinae* (Nesom 1993b). The first seven genera in Table 1 appear to be relatively closely related among themselves. *Aylacophora* and *Palaepappus* could justifiably be combined with *Nardophyllum*, and there is only weak justification for separating *Parastrephia* from *Lepidophyllum*. In the original description of *Hinterhubera*, Weddell (1855) recognized its resemblance to *Diplostephium*, and Blake (1922) very early observed that *Chiliotrichum* is closely related to *Diplostephium* and *Hinterhubera*. The relationship of *Llerasia* to these genera, however, has not been

previously recognized. *Llerasia* was included by Zhang & Bremer in the *Haplopappus* group, where it has been treated previously as sect. *Diplostephioides* (Hall 1928; Blake 1927), but it is a distinct genus (Cuatrecasas 1969, 1970; Dillon & Sagástegui 1988) with diagnostic features of the *Hinterhuberinae*. Its species are particularly similar to some of *Diplostephium* in their broad leaves and a corymbiform-cymose capitulescence. In recent studies (Nesom 1992, 1993a), I suggested that *Oritrophium* might be most closely related to the North American *Oreostemma* E. Greene, but with further perspective it now appears more likely that *Oritrophium* is a highly derived member of the *Hinterhuberinae* (its only herbaceous member); the possibility of such a relationship was earlier noted by Cuatrecasas (1961).

The North American *Aztecaster* is the only other genus of *Hinterhuberinae* besides *Hinterhubera* with peripheral pistillate flowers apparently modified from disc flowers, both genera also produce flattened achenes and pseudo-hermaphroditic central flowers, and both lack receptacular pales. The relatively close geographic approach of *Hinterhubera* to *Aztecaster* also suggests that they may be closely related. *Hinterhubera*, however, is specialized and different from *Aztecaster* in its very small, closely appressed leaves, vestiture that tends to be glandular, terminal, solitary heads, and 2-3 series of pistillate (peripheral) flowers with long lobes.

Among all the genera of the subtribe, *Ericameria* is the second most variable (in leaf morphology, indument, capitulescence form, achene morphology, presence/absence/reduction of ray flowers) - *Olearia* is even more variable. *Ericameria* has been divided into four sections (Nesom 1990a), but because of significant intergradation among these morphological groups and hybridization in a number of wide parental combinations, the genus has appeared to be monophyletic. Its internal structure and the possibility of polyphyly, however, should be reconsidered in view of its newly hypothesized generic position. The relationship of *Ericameria* within the subtribe is not clear, but there is no particular evidence besides geography that would suggest it is closest to *Aztecaster*, especially in view of the probable close relationship between *Aztecaster* and *Hinterhubera*. *Ericameria* fits the pattern of North American desert shrubs derived from evolutionary antecedents in South America (Johnston 1940; Raven 1963), and it is a reasonable hypothesis that it is derived from plants similar to the yellow-rayed, ericoid-leaved, bristle-pappose *Chilophyllum* of arid, montane regions of Argentina and Chile. These latter species, however, are specialized in several features that suggest *Ericameria* could not have been derived from them (*i.e.*, paleate receptacles, glandular achenes). In fact, the relationship of *Ericameria* to any New World genus appears to be so tenuous that it seems possible its origin in North America was from now-extinct Old World ancestors in the Madro-Tertiary flora (Raven & Axelrod 1978), which arrived via an Afro-Eurasian route (Tiffney 1985; Taylor 1985, 1990). Such also seems to be the case for several other groups of western North

American Astereae of essentially Madrean affinities, e.g., *Rigiopappus* A. Gray and *Tracyina* Blake and *Monoptilon* Torr. & Gray, *Chaetopappa* DC., and *Pentachaeta* Nutt., which appear to be more closely related to *Felicia* Cass. and *Amellus* L. than to any New World species of the tribe (Nesom in prep.). The early Tertiary age associated with their origin is not inconsistent with the potential age of the Hinterhuberinae and other basal groups of Astereae. Further, as noted by Raven & Axelrod (1974, p. 604), "Probably a majority of families and many modern genera of seed plants had come into existence by the Paleocene."

A close relationship between *Nardophyllum* and the South African genus *Pteronia* was observed by Cabrera (1954), and my studies support this view in a general sense. *Pteronia* is a member of the Hinterhuberinae, where it is somewhat isolated; it does not belong with the *Chiliotrichum* group. The analysis by Zhang & Bremer placed *Pteronia* (with *Engleria*) as a basal group in their heterogeneous Solidagininae. Following Engler (1888), they positioned *Engleria* as the sister genus to *Pteronia*, perhaps on the basis of opposite leaves produced by plants of both genera, but the evolutionary affinities of *Engleria* lie with *Felicia* and closely related genera (Nesom in prep.). In addition to the African *Pteronia*, five Madagascan species previously regarded as *Aster* but clearly within the Hinterhuberinae have been recognized as the separate genus *Madagaster* Nesom (Nesom 1993c). The yellow-rayed Madagascan endemic *Rochonia* also belongs in this subtribe; its resemblance to *Madagaster* has been discussed by Nesom (1993c) and earlier by Humbert (1932, 1960), who also noted the strong resemblance of both groups of Madagascan species to *Diplostephium* and *Olearia*.

The composition of the *Olearia* group, which includes the five Australasian genera listed in Table 1, has been discussed in various papers by Drury (1968), Given (e.g., 1969, 1973), and most recently by Nesom (1992, with regard to the relationship between *Celmisia* and *Oritrophium*, and 1993c, with regard to the definition of *Olearia* and its relationship to the Madagascan species). The genus *Remya* Hillebr. ex Benth., considered to be a member of the *Olearia* group (Wagner & Herbst 1987; Zhang & Bremer 1993), is here tentatively excluded from the Hinterhuberinae. Lander (1989) recently segregated a species from *Olearia* as the monotypic genus *Apostates* Lander, which he retained in the Astereae. *Apostates* is similar in habit to some members of Hinterhuberinae, but the combination of its short, apically truncate style appendages, narrowly tapering achene base, and tailed anthers suggest that it is a member of the Inuleae rather than the Astereae. The anther bases of some of the Hinterhuberinae are similar in morphology (see Drury 1968; Given 1973; Zhang & Bremer 1993), but Zhang & Bremer also expressed their reserve regarding the position of *Apostates* by listing it among "isolated genera."

In the recent analysis by Zhang & Bremer, *Chiliotrichum*, *Olearia*, and *Hinterhubera* were positioned together as a subgroup of their subtribe Asteri-

nae (Fig. 3), united by "anther bases cordate or sagittate" and shrubby habit (although only *Hinterhubera* of their *Hinterhubera* group is shrubby). I do not consider the species represented here to be part of the Asterinae, which is a group almost wholly of the Northern Hemisphere (Nesom in prep.), although the two subtribes may be closely related. A more basal position within the tribe for the *Hinterhuberinae* is emphasized by its apparently ancient geographic distribution.

REDEFINITION OF THE SUBTRIBE BACCHARIDINAE

The only other primitively shrubby group of Astereae besides the *Hinterhuberinae* is the *Baccharidinae*, which also has a major disjunction between Africa and South America, but the two subtribes apparently are not particularly closely related. The *Baccharidinae*, whose definition here differs from any previous ones, comprises the American genera *Baccharis* L. (tentatively including *Baccharidastrum* Cabrera, *Baccharidopsis* Barroso, and other segregates), *Archibaccharis* Heering, and *Heterothalamus* Less. and the Afro-Asian *Microglossa* DC., the Afro-Madagascan *Psiadia* Jacq., the Madagascan *Psiadiella* Humbert and *Vernoniopsis* Humbert, and the Mascarene *Sarcanthemum* Cass. Zhang & Bremer's cladistic analysis of the Astereae (1993) placed the American genera as the sister group to the *Psiadia* group (including *Microglossa*, *Psiadia*, and *Psiadiella*, *Sarcanthemum* and two other extraneous genera), and positioned these together in a highly advanced position within their Asterinae. In contrast, I regard the *Baccharidinae* as a primitive group within the tribe (Nesom in prep.). *Psiadia* has sometimes been positioned with *Conyza* L. (e.g., by Hoffmann 1890 in the *Conyzinae*), but plants of *Conyza* and its close relatives are herbs with markedly different vegetative, floral, and fruit morphology. Zhang & Bremer placed *Vernoniopsis* in a group with the endemic Madagascan genus *Apodocephala* Baker, which I regard as an isolated, basal element of the Astereae.

Plants of the *Baccharidinae* are shrubs or small trees with small heads in a corymbose capitulescence, disc corollas with deeply cut, reflexing-coiling lobes, pistillate flowers with reduced corollas (pistillate flowers absent in *Vernoniopsis*) and commonly in several series, small achenes that are multinerved, rarely glandular, and essentially terete (though sometimes flattened, e.g., see Scott 1990), and there is a distinct tendency for the leaves to be punctate-glutinous. The central flowers are functionally staminate in *Psiadia*, *Psiadiella*, *Sarcanthemum*, some species of *Microglossa*, and in almost all of the New World species. Dioecy or a related condition is invariably characteristic of the New World species. Hypotheses regarding various pathways in the development of dioecy in the *Baccharidinae* have been recently discussed (Hellwig 1990; Zanolwjak 1991), but a broader hypothesis of the composition of the subtribe has not been previously put forward.

DEVELOPMENT OF DIOECY IN AZTECASTER

Dioecy in the Baccharidinae and in *Aztecasteer* appears to have developed along two different pathways. In the ancestral Baccharidinae (the primarily Afro-Madagascan genera), heads are heterogamous with pistillate (peripheral) and staminate (central) flowers, the latter usually pseudo-hermaphroditic with sterile ovaries. The staminate flowers are of typical hermaphroditic morphology, actinomorphic with five apical lobes, but the style branches of these flowers lose the stigmatic lines, sometimes becoming connate for part of their length. The pistillate flowers are fertile and appear to be homologous with those in the rest of the tribe. The Baccharidinae pistillate corolla is unvascularized and commonly produces a short ligule that equals or exceeds the involucre bracts, but it is often merely an apically truncate or fimbriate tube.

The ovarian sterility of the American Baccharidinae is here interpreted as a trait or tendency inherited from an ancestor in common with their Old World relatives. In *Baccharis*, where dioecy and monoecy prevail, a single head produces only pistillate or staminate flowers; in *Archibaccharis*, the segregation of the sexes is incomplete, and the condition is referred to as polygamo-dioecious. The pistillate heads, predominantly with pistillate flowers, almost always bear a few, central flowers of hermaphroditic morphology that may or may not produce fertile ovaries (Jackson 1975). The staminate heads, predominantly with staminate flowers, more rarely produce a few peripheral, pistillate flowers. It seems clear that in the Baccharidinae, the dioecious condition has been preceded by loss of fertility (at least partially) in the ovaries of the central flowers and then has occurred as a result of the loss of either the pistillate or staminate flowers within a single head.

Dioecy appears to be strict in *Aztecasteer*, with the heads either completely staminate or completely pistillate. The staminate (pseudo-hermaphroditic) flowers in these plants are morphologically and functionally similar to those of the Baccharidinae, and their ovarian sterility (or tendency for it) probably has been inherited in common with that of its close relatives in the Hinterhuberinae (i.e., *Diplostegium*, *Hinterhubera*). The pistillate flowers of *Aztecasteer*, however, appear to be derived from typically hermaphroditic ones by a reduction in size and loss of the stamens. These pistillate corollas are tubular, regular, and with five, distinct, apical lobes, and although the five vascular traces do not reach the lobes, they do extend from the corolla base about halfway up the tube. There is a propensity in the Hinterhuberinae for the loss (in *Ericameria*, the *Chiliotrichum* group, *Llerasia*) or reduction (in *Ericameria*, *Lepidophyllum*, *Parastrephia*, *Hinterhubera*) of ligulate flowers. This makes it a reasonable hypothesis that the species ancestral to *Aztecasteer* produced discoid heads bearing only actinomorphic, hermaphroditic flowers (ovaries fertile), without any peripheral, ligulate, pistillate flowers.

Cuatrecasas (1969) observed that aspects of the floral biology of *Diploste-*

phium suggest an approach to dioecy, almost certainly referring to the tendency for ovarian sterility in the central flowers and to earlier observations by Blake (1928). Blake noted that in *D. schultzei* Wedd., the number of pistillate (peripheral) and of pseudohermaphroditic (central) flowers is highly variable, with both tending to be highly reduced, and in some plants, the heads produced only pistillate, ligulate flowers, a condition clearly approximating or approaching dioecy or polygamo-dioecy. Humbert (1960) has observed a similar phenomenon in post-fire regrowth of plants of *Rochonia*.

A hypothesis for the independent derivation of dioecy in the *Hinterhuberinae* and *Baccharidinae* receives support from recent studies of restriction site variation in chloroplast DNA. In these studies, *Baccharis* is only distantly related to *Ericameria* within the *Astereae* (Suh 1989; Morgan 1990; and see Nesom *et al.* 1990 for a summary). Although dioecy, or some close approach to it such as monoecy or polygamo-dioecy, is the rule in American *Baccharidinae* and appears to be a heritable condition, there are no other dioecious species in the *Astereae* and it is an uncommon phenomenon in the rest of the family as well (Bentham 1873). Dioecy was not mentioned in any of the various taxonomic or biological discussions in Heywood *et al.* (1977) for any tribe of *Asteraceae*.

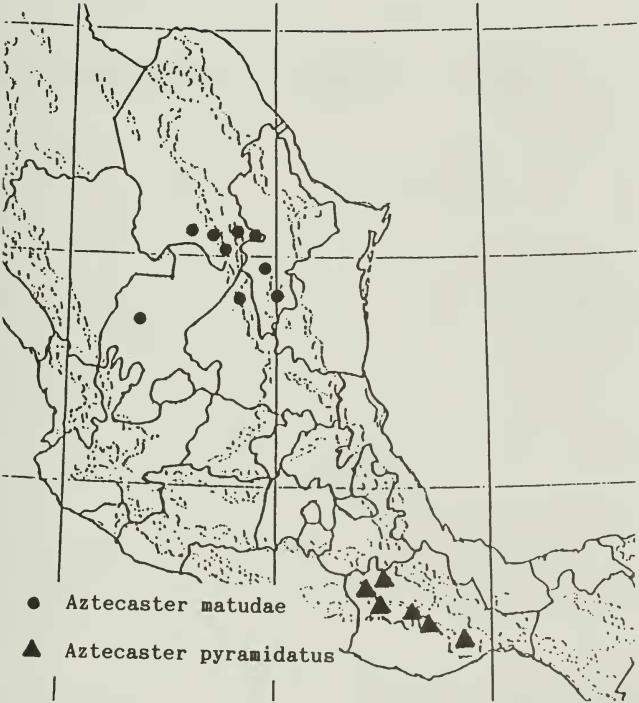
TAXONOMY

Baccharis pyramidata and *B. matudae* are formally segregated here as a new genus, named for the indigenous people of the area where it is endemic and echoing the apparent intent of Robinson & Greenman when they formulated the epithet of the original species. There is nothing obviously "pyramidal" in the morphology of these species. The new genus is compared in the diagnosis to *Ericameria*, its nearest geographic relative.

Aztecaster Nesom, *gen. nov.* TYPE SPECIES: *Aztecaster pyramidatus* (B. Robins. & Greenm.) Nesom.

Speciebus Ericameriae Nutt. ut videtur similis sed differt foliis ericoideis, capitulescentia laxe spicata, capitulis foliis proxime subtentis, phyllariis costam aurantiacam ac appendicem apicalem vel apiculum carentibus, achaeniis plerumque 2-nervatis, et praesertim statu sexuali dioecio.

Shrubs 0.5-1.6 m tall, with rigid, straight branches, the young stems densely and closely silvery-white pannose, glabrate with age. Leaves densely arranged along the stems, commonly with axillary fascicles, lightly flocculent, quickly glabrescent, usually glutinous but without visible glands, linear-oblong, 4-20



Map 1. Distribution of *Aztecaster pyramidatus* and *A. matudae*.

Table 1. Composition of the subtribe Hinterhuberinae and the continental distribution of the genera. The numbers in parentheses refer to the number of species in the genus.

HINTERHUBERINAE Cuatr., *Webbia* 24:5. 1969. TYPE GENUS: *Hinterhubera* Sch.-Bip. ex Wedd.

Chiliotrichopsis Cabrera (3).

Chiliophyllum Phil. (3).

Aylacophora Cabrera (1).

Paleaeppus Cabrera (1).

Nardophyllum Hook. & Arn. (7).

SOUTH AMERICA

Lepidophyllum Cass. (1).

Parastrephia Nutt. (5).

Chiliotrichum Cass. (2).

Diplostephium Kunth (ca. 90, 1 sp. in Costa Rica).

Oritrophium (Kunth) Cuatr. (ca. 15, 1 sp. in México) (tentatively included in the subtribe).

Llerasia Triana (14).

Hinterhubera Sch.-Bip. ex Wedd. (8 or 9).

Aztecaster Nesom (2).

Ericameria Nutt. (31).

NORTH AMERICA

Olearia Moench (ca. 100).

Celmisia Cass. (ca. 60).

Pleurophyllum J.D. Hooker (2-3).

AUSTRALASIA

Damnomenia Given (1).

Pachystegia Cheeseman (1).

Pteronia L. (ca. 80).

SOUTH AFRICA

Rochonia DC. (4).

Madagaster Nesom (5).

MADAGASCAR

(-26) mm long, 1-2 mm wide, entire, ericoid with strongly revolute margins and the midvein strongly raised on the abaxial surface. Heads sessile in leaf axils, in an open cylindric-spicate capitulescence, each head immediately subtended by a cluster of leaves; each head either with functionally pistillate flowers or functionally staminate flowers, the pistillate and staminate heads on separate plants and the species dioecious; pistillate involucres 6-8(-10) mm long, 4-6 mm wide, the staminate heads slightly smaller; phyllaries stramineous to greenish-yellow, prominently resinous from biseriate glandular hairs, the inner portion strongly indurated and of similar texture from base to tip, narrowly keeled from base to tip or not, narrowly triangular to narrowly ovate, (0.5-)0.8-1.5(-1.8) mm wide including the narrow to broad scarious margins, in 3-4 imbricate series strongly graduated in length with the outermost ca. 1/3 as long as the inner; receptacle slightly convex, barely alveolate. Staminate (pseudohermaphroditic) flowers with abortive ovaries, 8-9 per head, the corollas actinomorphic, ca. 4-7 mm long, the tube strongly delimited or not, the lobes 0.8-1.2 mm long, triangular, spreading to reflexing, style branches linear-lanceolate, 1.8-2.1 mm long, with short collecting hairs from base to apex, stigmatic lines absent, the vascular trace not at all thickened. Pistillate flowers 5-10 per head, the corollas actinomorphic, narrowly tubular, 4-6 mm long, with 5 lobes 0.5-1.0 mm long, the style branches 1.8-2.0 mm long, with stigmatic margins extending completely around the periphery of each branch; achenes tan, oblong-obovate, flat with a nerve at each margin or sometimes with an additional nerve in the middle of one or both faces, 2.5-3.0 mm long, 0.7-0.9 mm wide, moderately to densely strigose with duplex hairs (Zwillingshaare), eglandular; pappus of ca. 35-50 barbellate bristles with attenuate apices, in essentially a single series. Chromosome numbers unknown but predicted to be $n=9$. Illustrations in Hall & Clements (1923, pl. 30) and Rzedowski (1972, Fig. 1).

KEY TO THE SPECIES

1. Abaxial midvein of leaves strongly raised and distinctly green, with a shallow central groove; central indurated portion of phyllaries ovate to narrowly ovate, 0.6-1.0 mm wide, stramineous but commonly green-tinged in the distal half, the midvein also often distinctly greenish distally, not raised as a keel; pistillate corollas 4.6-5.6 mm long, with lobes 0.6-1.0 mm long; staminate corollas 6.0-6.8 mm long, without a distinctly delimited tubular portion below the throat; the lobes 1.3-1.5 mm long and slightly spreading but not recurving, staminate style branches 2.5-3.0 mm long; Oaxaca. *A. pyramidatus*
1. Abaxial midvein of leaves somewhat raised but not green or strongly conspicuous; central indurated portion of phyllaries linear-lanceolate, 0.3-

0.6 mm wide, completely stramineous, with a narrow, raised keel from base to apex; pistillate corollas 3.8-4.8 mm long, with lobes 0.4-0.6 mm long; staminate corollas 3.5-5.0 mm long, the tube 2.0-2.2 mm long and strongly delimited and abruptly expanded into the throat, the lobes 0.8-1.0 mm long and spreading-recurving, staminate style branches 1.8-2.0 mm long; San Luis Potosí, Zacatecas, Coahuila, and Nuevo León.
 *A. matudae*

Aztecaster pyramidatus (B. Robins. & Greenm.) Nesom, *comb. nov.* BASIONYM: *Bigelovia pyramidata* B. Robins. & Greenm., Proc. Amer. Acad. Arts 32:43. 1896. *Chrysothamnus pyramidatus* (B. Robins. & Greenm.) Hall & Clements, Publ. Carnegie Inst. Washington 326:197. 1923. *Haplopappus pyramidatus* (B. Robins. & Greenm.) Blake, Contr. U.S. Natl. Herb. 23:1491. 1926. *Baccharis pyramidata* (B. Robins. & Greenm.) Rzed., Brittonia 24:398. 1972. TYPE: MEXICO. Oaxaca: hills above Oaxaca, 5500 ft, 16 Nov 1894, C.G. Pringle 6048 (HOLOTYPE: GH!; Isotypes: MO!, UC, US!).

Grassland to matorral, 1600-2350 m; flowering November-March.

Additional specimens examined: MEXICO. Oaxaca: Sierra entre Oaxaca y Tehuantepec; 22 Dec 1968, Boege 1047 (GH); Cañon of the Río Tlahuitoltepec, 19-27 Feb 1937, Camp 2715 (A); Cerro Santo Domingo, 22 Dec 1906, Conzatti 1645 (MEXU); Dist. Centro, El Fortín, 1650 m, 11 Feb 1933, Conzatti 4913 (LL); Monte Alban, 1850 m, 3 Mar 1937, Conzatti & Camp 5239 (MEXU); Dist. Coixtlahuaca, Cerro del Agua, 3.5 km NNW of Concepción Buenavista, 2350 m, 3 Feb 1969, Cruz 2325 (ENCB, TEX); 8 km SW of Tlaxiaco, 1900 m, 7 Feb 1965, McVaugh 22298 (ENCB); Dist. Coixtlahuaca, 2 km NNE of San Mateo Tlapiltepec, 2200 m, 11 Jan 1969, Rzedowski 26676 (ENCB, WIS); Monte Alban, cerca de Oaxaca, 1850 m, 27 Feb 1972, Rzedowski 28827 (ENCB) and 28828 (ENCB, TEX); Portillo San Dionisio, 62 km ESE de Oaxaca, sobre el camino a Tehuantepec, 19 Dec 1972, Rzedowski 30012 (MO) and 30013 (MO); Cañada Sta. María, 8 Dec 1895, Sailor 1477 (GH, MEXU); Monte Alban, 23 Nov 1894, Smith 371 (MO); Monte Alban, ca. 8 km NW of Oaxaca, 28 Dec 1976, Turner P-48 (LL); 1 km por la desviación a Acaquiza-pán, on the Huahuapan de León-Tehuacan highway, 20 Feb 1986, Villaseñor 911 (MEXU, TEX); ca. 24 mi from Mitla on road to Totontepec, 11 Jan 1989, Woodruff 227 (MO, TEX).

Aztecaster matudae (Rzed.) Nesom, *comb. nov.* BASIONYM: *Baccharis matudae* Rzed., Brittonia 24:398. 1972. TYPE: MEXICO. Zacatecas: 5 km al NE de Chalchihuites, 2100 m, orilla de camino, 2 Apr 1957, J. Rzedowski 8758 (HOLOTYPE: ENCB!).

Grassland to matorral and open pinyon pine woodland, ca. 1800-2700 m; flowering February-July.

Additional specimens examined: MEXICO. Coahuila: Sierra Zapaliname, 2480-2600 m, 25 Mar 1990, *Hinton et al. 20225* (TEX) and *20231* (TEX); Carneros, 12 Jul 1934, *Pennell 17302* (GH,US); Sierra de Parras, *Purpus 1326* (UC, as cited by Hall & Clements 1923); E of Saltillo, 6.8 mi E of San Juan de Los Dolores toward La Jacinta, 7600 ft, 17 Dec 1989 (sterile), *Schoenfeld & Fairey 35* (TEX). Nuevo León: Ca. 15 mi SW of Galeana, Cieneguillas to Pablillo by the upper trail, 17 Jun 1934, *Mueller 875* (TEX); 15 mi S of km 168 on Hwy 61, N of Dr. Arroyo, 2140 m, Jul 1982, *Vankat 98* (TEX). San Luis Potosí: Tierras Negras, 12 km S of Mineral de Catorce, 2700 m, roadside, 3 Feb 1956, *Rzedowski 7278* (ENCB).

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